

THE ANNALS

AND

MAGAZINE OF NATURAL HISTORY.

[THIRD SERIES.]

No. 90. JUNE 1865.

XLVI.—*On a new Form of Alternation of Generations in the Medusæ, and on the Relationship of the Geryonidæ and Æginidæ.* By Dr. ERNST HÆCKEL*.

THE fact of the alternation of generations between the Medusæ or Discophorous Acalephs and the Hydroid polypes, which when first made known excited so much attention, and was doubted by so many, has in the two last decennia been proved, by widely extended investigations, to be so generally diffused in the class of the Hydromedusæ, that the cases of simple homogonic reproduction in this class of animals appear to constitute rare exceptions. At the same time, an unexpected abundance of the most various modifications has been discovered, rendering the reproductive conditions of these animals the most interesting in the whole organic world. But that this abundance is still by no means exhausted is proved by almost every thorough investigation of a particular group of Medusæ. Thus the careful investigations which I had the opportunity of making during a long period last spring, in the Gulf of Nice, upon a large *Geryonia*, and of continuing up to the present time upon well-preserved preparations, have led me to the discovery of a new form of alternation of generations, which differs so much from all other known forms that it is certainly permissible to give a short preliminary account of it here.

The *Geryonidæ* form a family of the Craspedota or *Medusæ cryptocarpæ*, which, although small, is strikingly distinguished by many remarkable structural characters. The family may be divided into two subfamilies—the *Liriopides* and *Carmarinides*—of which the former (*Liriope*, *Glossocodon*) resemble most of the other Medusæ in the *quadruplicity* of all their organs, whilst the

* Translated from the 'Monatsbericht der Akad. der Wiss. zu Berlin,' Feb. 1865, p. 85, by W. S. Dallas, F.L.S.

latter (*Carmarina*, *Geryonia*) are distinguished by having all their organs *sextuple*, and by their considerable size. With regard to the conditions of reproduction in these animals, scarcely anything has hitherto been known. According to a short notice published by Krohn* in 1861, this most meritorious naturalist had, as early as 1843, observed a sexually mature female specimen of *Geryonia proboscidalis*, of which "the extremity of the peduncle, reaching down freely into the stomachal cavity, appeared thickly beset with buds in various stages of development. In the less developed buds only the umbrella and peduncle could be distinguished; the further advanced ones had developed not only the six tentacles, but also the marginal corpuscles." This isolated observation, which seems to have attracted but little notice, might have led, had it been followed out, to the discovery of the wonderful phenomenon which will be described immediately.

Besides this we have hitherto had only the admirable description of a singular metamorphosis observed by Fritz Müller, in 1859, in the larva of a quadruplex Geryonide of the Brazilian coast†. The origin of this larva, which was captured swimming freely in the sea, and which gradually became converted into the sexually mature *Liriope Catharinensis*, remained unknown. Hence it has been generally believed, although supported by no direct observation, that the *Geryonidæ*, like the *Trachynemidæ* and *Æginidæ*, are propagated homogenically, and without any alternation of generations.

The *Geryonidæ* which I had the opportunity of continuously observing at Nice belong to two very different species. The smaller species, *Liriope* (*Glossocodon*) *eurybia*, which occurs there in abundance, is quadruplex, and has an umbrella of 8–10 millim. in diameter. This species undergoes a metamorphosis very similar to that of *Liriope Catharinensis* described by Fritz Müller. The second, much larger and rarer species, which I have named *Geryonia* (*Carmarina*) *hastata*, is sextuplex, and attains a diameter of 50–60 millim.

In the sextuplex *Geryonidæ* a metamorphosis has not hitherto been observed. I have, however, been able to trace this in its whole course in numerous larvæ of *Geryonia hastata* captured in the open sea. The metamorphosis of the sextuplex *Carmarinides* takes place on the whole in accordance with the same laws as that of the quadruplex *Liriopides*, of course with the difference that all the organs make their appearance to the number of six or a multiple of six, instead of four or a multiple of four. The

* Wiegmann's Archiv, xxvii. 1. p. 169, note. See Annals, ser. 3. vol. ix. p. 8 (1862).

† *Ibid.* xxv. 1. p. 310.

globular larva first of all developes six solid radial subsidiary tentacles, then six solid interrarial tentacles, and afterwards six interrarial sensory vesicles. Then only do the six hollow radial primary tentacles make their appearance, and lastly, after these, the six radial sensory vesicles. The first twelve solid tentacles are then lost, and only the last six, the hollow radial primary tentacles, remain. At the same time the long stomachal peduncle, which was at first entirely wanting, is developed.

These sextuple larvæ, the metamorphosis of which into the fully-developed *Geryonia hastata* may be traced through all its stages, are probably the products of sexual reproduction. But the same animal also developes young Medusæ asexually, and, indeed, *by gemmation in the interior of the digestive stomachal cavity*; and these have a perfectly different form and structure. These Medusoid-buds are probably the same that Krohn saw on one occasion. But they are not, as stated by him, *sextuple*, nor do they become developed into a *Geryonia*; but they are *octuple*, and are developed into a totally different Medusa, very probably into a species of the family *Æginidæ*, described by me as *Cunina rhododactyla*.

This gemmation, which is exceedingly remarkable, both on account of its locality and of its heterogeneous product, occurs only in the stomachs of sexually mature animals, and in both sexes. I was able to examine twenty-three individuals of *Geryonia hastata* with regard to the conditions of this phenomenon. Of these no less than nine had the stomach reduced to a stump, or in course of reproduction. Of the other fourteen, seven showed a long spike of closely united eight-rayed buds in the stomach; of these seven animals three were males, and four females, all with perfectly mature sexual products in the genital leaves. The number of buds in the stomach of each animal varied from twenty to nearly a hundred. The buds were seated close together, with the vertical surface of the umbrella (the aboral pole) attached to a long cylindrical process which was fixed to the base of the stomach. This process is nothing but the long dagger-like prolongation of the stomachal peduncle, which, in *Carmarina*, as in *Glossocodon*, projects freely into the stomachal cavity, and in non-gemmiparous animals is often protruded from the mouth, and seems to subserve the function of a tongue. In two of the largest *Geryonia* I counted the buds attached to the tongue and forming with it a thick cylindrical spike, which hung down freely in the middle of the campanulate stomach like the clapper of a bell. One spike was composed of seventy-one, the other of eighty-five buds. Young and old buds, in the most various stages of development, are seated indiscriminately together.

The most developed, largest, and oldest buds have a thick disciform umbrella, rather more than 1 millim. in diameter, and are quite different both from the full-grown *Geryonia hastata* and from the youngest larvæ of that species, which also had umbrellas 1 millim. in diameter. *Geryonia hastata* develops all its organs in *sixes*; the buds, on the contrary, in *eights*. During its metamorphosis *Geryonia* develops three circles, each of six tentacles, the tentacles of each circle being quite different from those of the other two. The Medusa-buds, on the contrary, bear eight similar tentacles affixed in deep notches of the margin of the umbrella, half on the dorsal surface of the umbrella. Of the eight marginal lobes, which project far between the notches, each bears at its apex a sensory vesicle, which projects freely upon a short peduncle. In *Geryonia*, on the contrary, the margin of the umbrella is not divided into lobes, and the twelve sensory vesicles are completely enclosed within the gelatinous substance of the margin. Equally important differences are presented by the gastrovascular apparatus of the mature *Geryonia* and that of the buds produced in its stomach. In the former the small campanulate stomach is seated upon a long solid gelatinous peduncle, in the surface of which six separated canals, originating from the base of the stomach, ascend to the umbrella, on reaching which they are bent round, and run in the subumbrella as radial canals to the margin of the disk. Here the six canals are united by a circular annular vessel, from which seven cæcal centripetal canals are given off in a radial direction inwards between each pair of radial canals. In the buds, on the contrary, there is a perfectly simple, rather long, cylindrical stomachal tube, which leads into eight broad and flat radial sacs reaching to the base of the tentacles. These stomachal sacs are united by an annular vessel, which runs along the margin of the eight lobes.

That the singular buds which sprout from the tongue of the *Geryonia* within the stomachal cavity cannot themselves be developed into *Geryoniæ* is perfectly evident. By no metamorphosis could this bud, which is so completely different in the fundamental structure of its body, revert directly to the form of the parent animal. Nor, from its whole structure, can it be converted into a quadruplex Geryonide. Nothing remains, therefore, except to seek the further stages of development of the buds in some other family of Medusæ. There is, however, only a single group of Medusæ which shares the above-mentioned very characteristic peculiarities of structure with the buds of *Geryonia*. This is the family of the *Æginidæ*. A species of this family, *Cunina rhododactyla*, occurs in great quantities in company with *Geryonia hastata*; indeed I have captured this *Cu-*

nina only on those days when the *Geryonia* also appeared in the Gulf of Nice, but then always accompanying the latter in great quantities.

The youngest individuals of *Cunina rhododactyla* that I have observed, of which the umbrella was 3 millims. in diameter, agreed in all essential particulars so closely with the oldest observed *Geryonia*-buds of 1 millim. diameter, that I can no longer doubt the identity of the two forms. As in the bud of the *Geryonia*, the thick disciform umbrella is divided at the margin by eight deep notches into the same number of lobes, each of which bears at its apex a pedunculate free sensory vesicle. Eight similar tentacles are attached in the notches. The simple unpedunculated stomach gives off from its circumference eight flat and broad radial sacs, which reach to the base of the tentacles, and are there united by a narrow annular vessel which runs along the border of the marginal lobes. The only difference, besides the smaller size and plumper form of the stomachal buds of *Geryonia*, that I can find between the oldest of these buds and the youngest individuals of *Cunina* consists in the fact that the tentacles of the latter are more slender and longer, and, on the other hand, the stomach is flatter and shorter—differences which would, no doubt, disappear by the observation of the intermediate age 2 millims. in diameter.

I have also been able to ascertain the further development of *Cunina rhododactyla* to full sexual maturity. It consists essentially in the gradual increase of the number of similar segments composing the body from eight to sixteen, a new segment being inserted from time to time between those previously existing. The oldest animals have an umbrella 10–11 millims. in diameter, and possess sixteen tentacles, sixteen stomachal sacs, sixteen marginal lobes, and a great but indeterminate number (between 50 and 100) of sensory vesicles. The latter increase in a very irregular manner, so that the different marginal lobes of one and the same animal bear from four to eight vesicles. The sexual products are developed in the lower wall of the stomachal sacs, from its epithelium.

From all that has been stated, it appears to me to be no longer doubtful that the octoradiate buds which sprout from the tongue of the sexually mature sexradiate *Geryonia* (*Carmarina*) *hastata*, within its stomachal cavity, are really developed directly into the sexually mature animal of *Cunina rhododactyla*. Should this supposition (which I cannot but regard as a certainty) be confirmed, it requires nothing further to show that we have here an exceedingly wonderful and perfectly and fundamentally new form of the alternation of generations, if indeed we may apply that name to this singular process. It might better be called

heterogonism or *alloëogenesis*. It is not, as in the other multifarious forms of the alternation of generations, a sexual and an asexual form—a Medusa and a polype—that stand in a reciprocal genital relation to each other; but we find here that a perfectly developed Medusa, evolved by metamorphosis from a larval form, at a time when its generative organs furnish mature products (from which probably the above-mentioned larvæ are produced), produces young Medusæ, asexually, by formation of buds in its stomachal cavity, and these are developed into a Medusa-form perfectly distinct from their parent, and which in its turn becomes sexually mature.

What, then, becomes of the sexual products of *Cunina*? How does this octoradiæ *Æginide* revert to the sexradiæ *Geryonide*? Or does it only propagate in an *Æginide* form? or are the larvæ of the *Geryonia* produced sexually or asexually from the *Cunina*? But, also, what becomes of the sexual products of the *Geryonia*? Does the *Cunina* also propagate asexually? or are there Hydroid polypes which establish the union between the two Medusoid forms, which appear to be so widely separated? These and many other questions force themselves upon us in the presence of this wonderful fact, without our seeing at present any way of escaping from this labyrinth. But I hope shortly to be able to take these questions in hand again at the Mediterranean, and to bring them to a solution.

The paradoxical nature of the demonstrated relation might well lead us to a suspicion of *parasitism*. But, leaving out of consideration other pertinent reasons to the contrary, this is at once contradicted with certainty by the fact that the development of the *Cunina*-buds upon the surface of the tongue of the *Geryonia* may be traced through all stages from its first commencement. The first foundation of the sprouting bud is nothing but a small disciform thickening of the epithelium of the tongue. This homogeneous cell-growth is then differentiated into two distinct laminæ—a lighter ectoderm and a darker endoderm. In the latter is produced a small round cavity, the first trace of the stomachal cavity, which then grows out into the above-mentioned cylindrical stomachal tube, whilst the disk is differentiated into eight segments.

The *Æginidæ* and *Geryonidæ* have hitherto passed as perfectly distinct families of Medusæ. The numerous peculiarities which so strongly characterize both the external form of the body and the interior structure of the *Æginidæ* appear, indeed, to remove this family far from all others. Quite recently, in fact, two distinguished naturalists have even separated the *Æginidæ* altogether from the great section of the Craspedota (*Cryptocarpæ*). Fritz Müller has placed them as a third distinct primary group

between the two other groups of the Craspedota and Acraspeda. Agassiz, on the other hand, has actually transferred them to the Acraspeda (*Phanerocarpæ*).

A very careful anatomical and histological investigation which I made, after becoming acquainted with the genetic relations just described, of two *Æginidæ* (*Cunina rhododactyla* and *C. albescens*) and two *Geryonidæ* (*Carmarina hastata* and *Glossocodon Eurybia*), led me to the surprising result that these two families present a far more essential agreement in internal structure than could be supposed from the remarkably different external form of the body. I shall only mention, in conclusion, the most important agreements, in a few words. It is regarded as the principal character of the *Æginidæ* that they have no annular vessel like the other Craspedote Medusæ, but merely blind sacs which issue from the circumference of the stomach. But these sacs are nothing but greatly dilated radial canals; and, in fact, they are united at the base by an annular vessel, which runs along the margin of the mantle, and has hitherto escaped the notice of observers merely on account of its very small dimensions. The intimate structure of this annular vessel is exactly the same as in *Geryonia*. As in that genus, so also in *Cunina*, there is, immediately beneath the annular vessel, a slender cylindrical or semicylindrical cartilaginous band, from which issue a number of centripetal and likewise cartilaginous bands, which rise in a radial direction for some distance in the outer surface of the margin of the mantle, and give support to it. Moreover, in *Cunina* as in *Geryonia*, there is a fine nervous ring on the margin of the umbrella, contiguous internally to the insertion of the velum, superiorly to the lower margin of the annular vessel, externally to the gelatinous substance of the mantle, and inferiorly to the cartilaginous ring. The formation of the sexual products in flat, leaf-like, saccular dilatations of the radial canals is also exactly accordant in both the families of *Æginidæ* and *Geryonidæ*, and very different from that occurring in all other Medusæ.

But the anatomical relation between *Cunina* and the larva of *Geryonia* is far greater than between the mature animals of the two genera. These two forms possess in common especially the characteristic firm habit of the umbrella and the peculiar structure of the solid, rigid tentacles, which are wanting in the mature *Geryonia*. The primary mass of these tentacles is formed by a cartilaginous cylinder, which is covered by a muscular tube; over this is an epithelium, in which urticating cells are here and there developed. The stomach of the young larva of *Geryonia* is also a very shallow sac, as in *Cunina*. The most essential anatomical difference between the *Geryonidæ* and

Æginidæ is to be found in the position and structure of organs of sense (marginal vesicles), which are certainly very different in the two families (and also as regards their intimate structure). In the *Æginidæ* the sensory vesicles are situated freely on the outer margin of the umbrella, and are elevated upon short peduncles. In the *Geryonidæ*, on the contrary, they are enclosed in the gelatinous mass which forms the lowest margin of the mantle, and each vesicle is seated here upon a ganglion-like enlargement of the nervous ring. Perhaps the demonstration of this close anatomical affinity of the *Geryonidæ* and *Æginidæ* may serve, at least in one respect, to make the genetic connexion of the two families above described appear less enigmatical.

Finally, I may remark that I had the pleasure of bringing the above-described remarkable phenomena under the immediate notice of one of the first authorities upon Medusæ, my friend Professor Gegenbaur, and that he was convinced of the correctness of my observations and the justness of the conclusions founded upon them.

XLVII.—*Notices of British Fungi*. By the Rev. M. J. BERKELEY, M.A., F.L.S., and C. E. BROOME, Esq.

[Continued from p. 404.]

[Plates XV., XVI., XVII.]

1063. *Peziza* (*Geopyxis*) *carbonaria*, Alb. & Schw. p. 314.

On burnt ground. Ascot, C. E. Broome, 1863.

A charming addition to our list.

PLATE XV. fig. 15. *a.* ascus with paraphysis, magnified; *b.* sporidia, more highly magnified.

1064. *P.* (*Humaria*) *Wrightii*, Berk. & Curt. Cupulis hemisphæricis, demum planis, coccineis, extus furfuraceo-granulatis; sporidiis globosis, l. subglobosis, junioribus lævibus, adultis echinulatis.

On trunks of trees covered with *Hypnum serpens*. Bodelwyddan, Flintshire, March 1864.

Sporidia .00045–.0006 inch in diameter; paraphyses slender, branched.

The Texas plant is just the same, and agrees exactly in habit.

PLATE XV. fig. 16. *a.* asci, magnified; *b.* paraphysis; *c.* sporidia, more highly magnified.

1065. *P.* (*Sarcoscyphæ*) *theleboloides*, A. & S. p. 321, t. 12.

On spent Hops. Batheaston, Ilford, Essex, C. E. Broome and W. W. Saunders.